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Decay curves of leaf litter from evergreen and deciduous tree species (*)

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ABSTRACT

The shape of the weight loss curve of leaf litter during the decay process was studied. Most of the curves obtained can be fitted well to composite exponential or asymptotic models which assume the existence of two decay phases with different decomposition rates. However, in certain cases these models are altered by the limiting environmental factors acting in different sequences. The shape of the decay curve is clearly different in deciduous and mediterranean evergreen species (with leaf abscission at the beginning of the dry period) due to the different environmental conditions during the initial decay period. We also evaluated the action of different environmental conditions which act permanently in zones with or without tree covering.

KEY-WORDS: Quercus rotundifolia - Quercus pyrenaica - *Leaf litter - Decomposition - Labile fraction - Refractory fraction.*

RÉSUMÉ

On a étudié la courbe de perte de poids de la litière de feuilles en fonction du temps pendant le processus de la décomposition. La plupart des courbes obtenues s'ajustent bien à des fonctions exponentielle double ou asymptotique, lesquelles indiquent l'existence de deux compartiments dont les vitesses de décomposition sont différentes. Cependant, dans certains cas, ces modèles théoriques sont modifiés par l'environnement. La forme de la courbe de décomposition est différente pour les espèces décidues et pour les espèces sempervirentes méditerranéennes (avec abscission des feuilles au commencement de la saison sèche) à cause des conditions différentes de l'environnement pendant la phase initiale de la décomposition. Nous avons aussi évalué l'action des divers facteurs de l'environnement qui agissent en permanence dans des zones avec ou sans couverture arborée.

MOTS-CLÉS : Quercus rotundifolia - Quercus pyrenaica - *Litière - Décomposition - Fraction labile - Fraction réfractaire.*

INTRODUCTION

Decomposition processes have received considerable attention in studies on terrestrial ecosystems as a consequence of the dominant detritus pathway in such ecosystems. One important task of such studies is the description of the seasonal variations in the intensity of decay because such variations reflect not only the influence of the environmental variables but also the chemical nature of the decomposing material.

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Different mathematical models have been employed for the description of the shapes of decay curves. The exponential model (JENNY *et al.*, 1949; OLSON, 1963) is the classical approach and assumes that litter is homogeneous in the sense that all constituents of the detritus have an equal probability of decomposing at any given time (CARPENTER, 1981). These assumptions are probably erroneous and the exponential model has now been improved by more complex versions. MINDERMAN (1968) described the effect of different decay rates in the litter components. One suitable model for the representation of this situation would be a sum of exponential equations (two in the simplest case). Another possibility, suggested by HOWARD & HOWARD (1974), is that one of the litter components is not decayed; in this case the most suitable mathematical model would be an asymptotic equation.

These latter models have been shown to be adequate in studies carried out under controlled laboratory conditions (CARPENTER, 1982) and demonstrate the validity of the suppositions regarding the heterogeneous nature of the litter. However, under natural conditions the environmental variations in many cases override this course of decay, such that it is not surprising that the curves obtained in these conditions only rarely fit into the theoretical models proposed, as may be seen for example from some of the results of BOCOCK (1964), WITKAMP & OLSON (1963) and ANDERSON (1973).

In order to account for the influence of the sequence of action of the environmental variables on the shape of the decay curve, in this study we used leaf litter of *Quercus rotundifolia* Lam., an evergreen species, which therefore sheds its leaves almost continually throughout the year, though it has a maximum at the start of the summer (ESCUDERO *et al.*, 1985 *a*). Hence, it is possible to study several decay cycles beginning in the different seasons. For comparative purposes a typical pattern for temperate deciduous forests has been included, using leaves of *Quercus pyrenaica* Willd., a submediterranean deciduous oak, which has the main period of leaf abscission in November.

STUDY AREA AND METHODS

The study stands consisted of a very sparse population of *Quercus rotundifolia* (24 trees/ha) and another of *Quercus pyrenaica* (39 trees/ha). These savannah-like communities, man clearfelled, occupy huge extensions of western Spain, where they are exploited for free range livestock rearing. The canopy projection was 11.32 % of the total area in the *Q. rotundifolia* plot and 12.86 % in the *Q. pyrenaica* plot. The remaining surface was covered by a pasture with a predominance of the grasses *Agrostis castellana* B. et R. and *Bromus madritensis* L. The *Q. rotundifolia* site is at 40 km to the south of Salamanca (40°40′N, 2°25′W) at an altitude of 820-880 m a. s. l. The *Q. pyrenaica* plot is approximately at 80 km to the south-west of Salamanca (40°37′N, 2°42′W) with a mean altitude of 850 m a. s. l.

The climate of the area is marked by long, cold winters and short, hot and very dry summers. Mean annual temperatures range around 11-12° C for the two plots studied. Mean annual rainfall ranges around 500 mm for the area populated by *Q. rotundifolia* and around 600 mm for that occupied by *Q. pyrenaica*.

Determinations of soil pH, organic matter, C, total N and extractable P, Ca and K were carried out in three replicate samples from each plot according to the methods described in CHAPMANN & PRATT (1973), BREMNER (1960) and WALKLEY & BLACK (1934). Granulometry of the $<$ 2 mm diameter fraction was studied according to the Robinson pipette method. The soil characteristics of the stands are summarized in table I. The soils are cambisol on granite in the *Q. rotundifolia* plot and acrisol on schists in the *Q. pyrenaica* plot. These soils are acid and poor in almost all nutrients, with the exception of potassium.

TABLE I. — *Some physical and chemical properties of the soils from the two stands.*

Plot	Depth (cm)	Coarse sand (0.2-2 mm) (%)	Fine sand (0.02-0.2 mm) (%)	Silt (0.002-0.02 mm) (%)	Clay (< 2 mm) (%)
Q. rotundifolia	0-10	10.9	11.4	59.4	18.3
	40-50	4.6	5.1	76.6	13.6
Q. pyrenaica	0-10	8.8	39.5	35.5	16.2
	40-50	13.4	40.6	18.9	27.1

Plot	Depth (cm)	pH (H_2O)	Organic matter	N (²) (%)	C/N	P (¹) mg/100 g	Ca (¹) mg/100 g	K (¹) mg/100 g
Q. rotundifolia	0-10	5.5	5.48	0.300	10.6	0.36	83.6	19.37
	40-50	5.5	0.52	0.055	5.4	0.44	92.9	2.08
Q. pyrenaica	0-10	5.0	9.33	0.393	13.7	1.09	26.4	21.44
	40-50	5.1	0.81	0.050	9.4	0.36	26.4	4.29

(¹) Extractable.
(²) Total.

The leaves were taken from several trees in each of the stands. Before weighing and sample preparation the leaves were air-dried at room temperature to approximately 10 % moisture. The moisture concentration was then calculated by drying in an oven at 80° C for 24 h. Samples of a weight equivalent to 30 g of ovendry weight were introduced into litter-bags with a mesh size of 1 mm. In each of the stands two trees were chosen; for each of these, sets of 12 litter-bags were buried at a depth of about 5 cm at each of the following locations: under the canopies, under the edge of the canopies and in zones without tree cover. Owing to the smaller radius of the crowns only the first and last locations were used in the *Q. pyrenaica* plot.

Four sets of litter-bags of *Q. rotundifolia* leaves were used, and were placed in the soil at the end of March, June, September and December of 1979. A single set of *Q. pyrenaica* litter-bags was installed at the end of November of 1979. Replicate ($n = 2$) samples of each set were collected at monthly intervals over a year. The litter-bags were taken to the laboratory where the leaf litter was carefully cleaned to remove the mineral particles and the oven-dry weight (80° C) was determined.

The ash concentration was then determined by incinerating in a muffle furnace for 5 hr at 450° C. By subtraction, the weight of organic matter in each sample was calculated. The ash concentration of the samples increased from 3-4 % in the initial samples up to 8-14 % in the final ones.

Determinations of cellular content, hemicellulose, cellulose and lignin in the initial material (before decomposition) were carried out according to the method of Van Soest (GOERING & VAN SOEST, 1970). Nitrogen concentration was determined by the Kjeldahl method and phosphorus by colorimetry (ESCUDERO *et al.*, 1985 *a*).

Four series of data were available for *Quercus rotundifolia*; each belonging to one of the 4 cycles, which henceforth will be referred to as "spring cycle", "summer cycle", "autumn cycle" and "winter cycle". The sole *Q. pyrenaica* cycle will be referred to as "deciduous cycle".

The fitting of the linear, simple exponential, composite exponential and asymptotic equations was carried out at the Computer Centre of the University of Salamanca using the program P1R and P3R of the "Biomedical Computer Programs" package, edited by the University of California Press in 1979. The goodness of fit was checked by examination of residuals and the calculus of ratios of mean squares (DRAPER & SMITH, 1966).

RESULTS AND DISCUSSION

The chemical composition of the initial material is shown in Table II. The lignin concentration was found to be relatively low such that its effect on the decay rate would not be expected to be very important (BERG & STAAF, 1980). The influence of the nutrient levels is probably more marked.

TABLE II. — *Organic and mineral components of the fresh litter of each cycle.*

	Q. rotundifolia				*Q. pyrenaica*
	cycles				
	Spring	Summer	Autumn	Winter	Deciduous
Cellular content (*CC*, %)	56.3	59.4	57.7	57.5	57.8
Hemicellulose (%)	8.6	8.2	8.2	7.8	5.2
Lignin (%)	11.5	11.3	11.4	11.4	13.0
Cellulose (%)	23.6	21.1	22.7	23.3	23.9
N (%)	1.28	1.12	1.29	1.48	1.01
P (%)	0.084	0.084	0.090	0.102	0.066

The goodness of fit of the different regression lines applied to each of the cycles is shown in table III. Owing to the non-linearity of some of the models it is not possible to calculate the significance of the fit (DRAPER & SMITH, 1966). The ratios of mean squares (RMS) shown in the table do permit, however, comparisons between the different models; the lower the corresponding RMS, the better the fit. With the experimental design above described, it is possible to observe the differences in the shape of the decomposition curve caused by different sequences of action of environmental factors. In turn, the three locations ("below", "edge" and "outside") permit the observation of the shape of the decay curve under different environmental conditions.

With some exceptions, the models which provide the lowest RMS are the composite exponential and asymptotic ones. The main exceptions were the three series of samples belonging to the summer cycle: in them, the best-fit regressions were the linear and simple exponential ones. Also, the deciduous cycle in one case is best fitted to the simple exponential equation.

The goodness of the best-fit equations in each case may be considered satisfactory since the RMS do not normally exceed the value of reference F statistic, even for $p = 0.10$. This satisfactory fit may also be observed in fig. 1, which show the average ($n = 2$) weights of the successive samples of the "below crown" location together with the weights predicted by the best-fit equations in each case. Considerable proximity may be seen between the observed and predicted values (fig. 1). The signs of the residuals do not show any tendencies associated with the different phases of the decay time course, as demonstrated by the low absolute values of the serial correlation coefficients of residuals (table IV), which also shows that the equation chosen in each case is the most suitable.

Accordingly, the asymptotic and composite exponential equations seem to reflect the decomposition with time fairly well in most cases. This result supports the validity of the assumption of the influence of the heterogeneity of the chemical

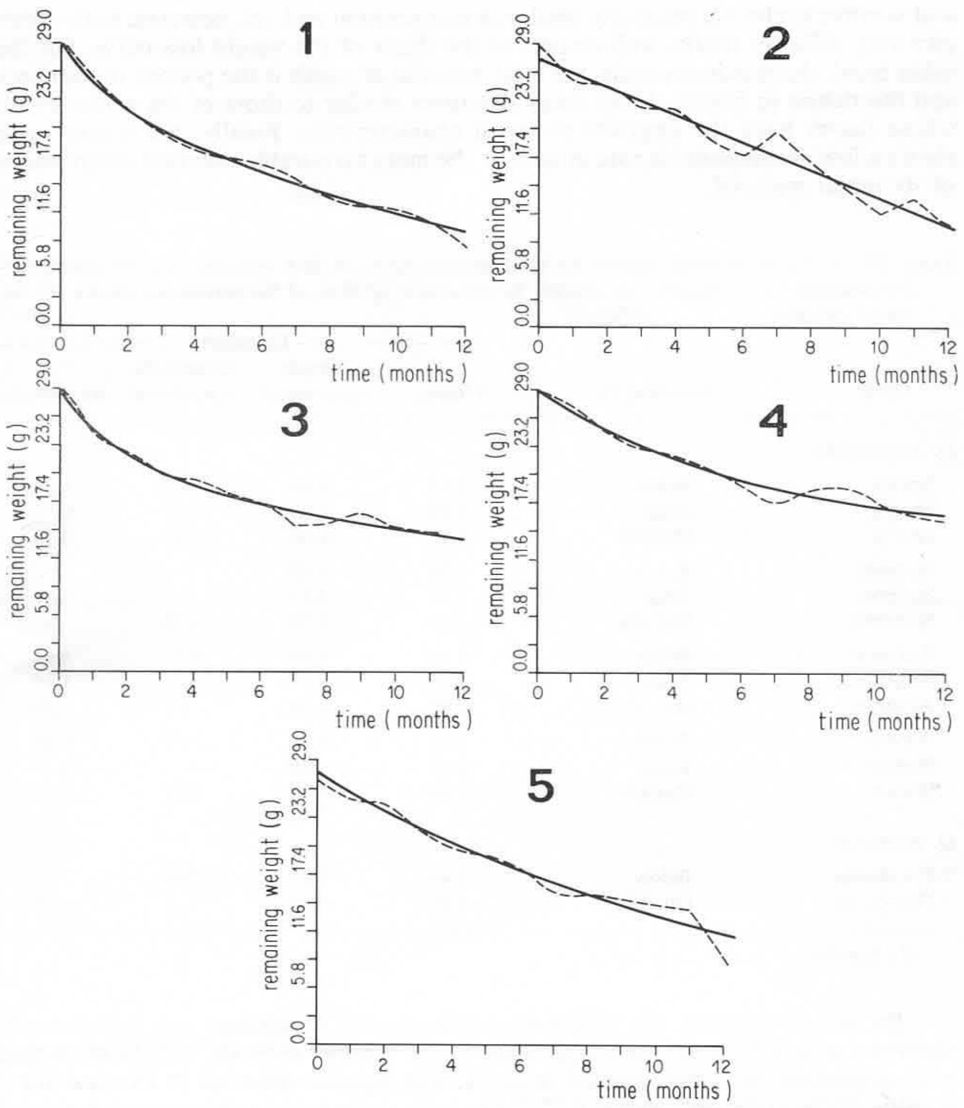

FIG. 1. — Observed (mean of 2 replicate samples) (dashed line) and predicted (full line) values for: 1) the spring cycle (from the composite exponential equation), 2) the summer cycle (from the linear equation), 3) the autumn cycle (from the composite exponential equation), 4) the winter cycle (from the asymptotic equation), 5) the deciduous cycle (from the simple exponential equation).

composition of the initial material on the shape of the litter decomposition curve (LOUSIER & PARKINSON, 1976). However, there are exceptions to this result. The differences in chemical composition of the starting material (table II) are unable to account for the differences between cycles because the leaves used in the spring

and summer cycles are relatively similar in composition and yet, however, both cycles give very different results with respect to the shape of the weight loss curve. On the other hand, the deciduous cycle, the start material of which is the poorest in nutrients and the richest in lignin, shows decay dynamics similar to those of the winter cycle, whose leaves have the opposite chemical characteristics. Finally, the winter cycle shows a low decomposition rate in spite of the more favourable chemical composition of its initial material.

TABLE III. — *Ratios of mean squares for the equations fitted. A dash indicates that the corresponding equation was converted into another by annulment of some of the parameters during the iteration process.*

Cycle	Location (1)	Equations			
		Linear	Simple exponential	Composite exponential	Asymptotic
Q. rotundifolia					
Spring	Below	2.15	0.89	0.42	0.84
Spring	Edge	6.19	2.30	0.47	0.72
Spring	Outside	18.96	10.30	0.92	4.76
Summer	Below	1.29	1.49	—	—
Summer	Edge	2.12	2.11	—	—
Summer	Outside	2.63	2.50	2.73	—
Autumn	Below	4.96	3.06	0.81	0.94
Autumn	Edge	2.29	1.13	—	1.10
Autumn	Outside	4.42	2.88	—	1.29
Winter	Below	1.07	0.72	0.47	0.44
Winter	Edge	2.32	1.76	—	0.53
Winter	Outside	3.98	3.50	2.18	2.06
Q. pyrenaica					
Deciduous	Below	2.44	1.94	2.08	—
Deciduous	Outside	3.69	2.47	—	1.95

(1) See text.

By way of contrast, the variations in the climatic conditions may satisfactorily account for the differences between cycles. In the summer cycle the initial time period is characterized by a pronounced drought. The rainfall collected in the first three months of the cycle only reached 77.7 mm with mean temperatures ranging around 20.9° C. The moisture content inside the litter-bags ranged, during these three months, between 2 and 42 %, while during the rest of the year values greater than 50 % were attained normally (ESCUDERO *et al.*, 1985 *b*). During these months the fauna found inside the litter-bags was very scarce and was limited to arthropod species with bodies designed to resist prolonged dry periods (GARRIDO & ESCUDERO, in press). The scarcity of fauna demonstrates the influence of the unfavourable environmental conditions on the overall biological activity, probably including microbial activity, which counteract the tendency towards a rapid catabolic decomposition of the fresh litter. The scarcity of rainfall, moreover, diminishes the importance of leaching during these months. In autumn the more favourable environmental conditions return, through an increase of rainfall, though they are accompanied by the usual

decrease in the litter quality experienced during the process of decomposition (Swift *et al.*, 1979). As a consequence, the summer cycle is lacking in any phase of very rapid decay, contrary to the other cycles.

The course of events characteristic of the summer cycle is the most normal under field conditions because most of the leaves of *Q. rotundifolia* are shed at the start of summer. In fact, in the majority of temperate forests leaf abscission occurs during the climatically most unfavourable periods for biological activity: winter for deciduous communities and the start of the dry season for mediterranean evergreen species. The limiting environmental conditions in these periods of the year may override the substrate quality regulation of the decay time course. In such conditions more or less pronounced deviations may be observed with respect to the models proposed, and such deviations may also be appreciated in the results presented in this work. The winters in the area studied are also relatively harsh, frequently reaching minimum temperatures of $-10°$ C. Such low temperatures negatively affect the decay of the winter and deciduous cycles during the initial phases. Accordingly, the decay curves of these cycles exhibit a less pronounced initial slope and are thereby rather closer to a straight line (fig. 1/4 and 1/5) compared with the spring and autumn cycles curves. In spite of this, all these curves exhibit a shape which points to the existence of an initial phase of rapid decay, different to the summer cycle. It is probable that the relatively rapid initial weight loss is due to leaching; the overall rainfall in the *Q. rotundifolia* plot during the first three months of the winter cycle rose to 91 mm with mean temperatures ranging around 5.3° C; the same measurements in the *Q. pyrenaica* plot gave 109 mm of rainfall in the first three months of the deciduous cycle with mean temperatures of 4.6° C. Evidently, percolation into the soil could be considerable and may remove soluble substances from the litter. The rainfall and temperature data for the summer months (see above) point to a lower availability of water percolating for the leaching process. A consequence of this is the low rate of weight loss of the litter during the first three months of the summer cycle (fig. 1/2).

Table IV shows the equations selected to represent the decay of each subset of samples, as well as the final residue (after a year of decay) predicted by each equation and the coefficients of serial correlation of residuals. A comparison may thus be made of the shape of the decay curve and of the decomposition rate in different environmental conditions (represented by the different locations).

The decomposition rate (measured by the final remaining weight) is generally greater below the edge of the canopies, somewhat lower under the crowns and clearly lower in the area outside the canopy cover. More detailed comparisons, including analysis of variance, between the different locations demonstrate the existence of significant differences between the decomposition rates of the different locations, the decay in the "below crown" location always being faster than that of the "outside" location (Escudero *et al.*, 1985 *b*). This latter finding agrees with the results of Whitford *et al.* (1981) and is probably due to the lower moisture content of these samples.

It is difficult to make further comparisons between the different locations in view of the diversity of equations chosen to represent decay. The assumptions implicit in the asymptotic and composite exponential models imply that two of the parameters of these equations represent the labile and refractory components of the decomposing material (Lousier & Parkinson, 1976). As shown in table IV, a single starting material may present weight loss equations with very different parameters, according

to location; that is, according to the environmental parameters to which the litter is exposed. This means that it is not possible in this case to assign concrete chemical components of the starting material to such parameters.

TABLE IV. — *Best-fit equation, predicted remaining weight* (PRW) *and serial correlation coefficient of residuals for each cycle.*

Cycle	Location (1)	Equation (2)	*PRW* (3)	*SC* (4)
Q. rotundifolia				
Spring	Below	$W = 3.85 \exp(-1.00\,t) + 24.12 \exp(-0.080\,t)$	33.05	−0.481
Spring	Edge	$W = 8.94 \exp(-0.57\,t) + 20.31 \exp(-0.068\,t)$	30.88	−0.390
Spring	Outside	$W = 7.23 \exp(-1.00\,t) + 21.85 \exp(-0.060\,t)$	36.63	0.392
Summer	Below	$W = 27.41 - 1.42\,t$	35.91	−0.181
Summer	Edge	$W = 28.27 \exp(-0.086\,t)$	34.93	0.207
Summer	Outside	$W = 28.16 \exp(-0.059\,t)$	48.14	0.143
Autumn	Below	$W = 7.59 \exp(-0.58\,t) + 21.16 \exp(-0.037\,t)$	46.76	−0.114
Autumn	Edge	$W = 23.08 \exp(-0.13\,t) + 5.42$	36.34	−0.212
Autumn	Outside	$W = 15.06 \exp(-0.22\,t) + 13.70$	51.26	0.013
Winter	Below	$W = 14.90 \exp(-0.16\,t) + 14.01$	56.20	−0.157
Winter	Edge	$W = 12.94 \exp(-0.28\,t) + 16.67$	59.51	−0.241
Winter	Outside	$W = 10.48 \exp(-0.30\,t) + 18.35$	64.86	0.277
Q. pyrenaica				
Deciduous	Below	$W = 27.76 \exp(-0.074\,t)$	40.14	0.187
Deciduous	Outside	$W = 17.35 \exp(-0.17\,t) + 10.80$	43.11	0.024

(1) See text.
(2) W = remaining weight; t = time in months.
(3) *PRW* = predicted remaining weight (% of the initial amount) for $t = 12$.
(4) *SC* = serial correlation of residuals.

CONCLUSIONS

The assumptions regarding the influence of the biochemical heterogeneity of the litter on the shape of the decay curve are probably correct, as shown in laboratory studies (CARPENTER, 1982). However, under field conditions, the climatic and other environmental factors often mask the tendencies implied by these models (SWIFT *et al.*, 1979). In the present work, it has been shown that the order of acting of the limiting factors causes changes in the shape of the decay curve. It is furthermore the course of events in temperate ecosystems (characterized by the coincidence of leaf abscission and the start of climatically unfavourable conditions) which most contributes to the modification of the shape of the decay curve with respect to what is proposed in the models. In deciduous temperate forests, the winter rainfall or the snow melt may, however, considerably intensify the weight loss in the initial phases of litter decay because of the relatively low sensitivity of decomposition to soil temperatures (JANSSON & BERG, 1985), thereby increasing the curvilinearity of the decay curves. This feature has been observed in our winter and deciduous cycles. On the other hand, in mediterranean ecosystems the environmental conditions at the start of decay are unfavourable both for the leaching of soluble material and for

catabolic decomposition, and probably straighten out the weight loss curve. Decomposition thus becomes more gradual, without the usual pulses at the start of the process. These differences between deciduous and mediterranean evergreen species are thus added to a more or less gradual leaf fall of these latter species (MONK, 1966) to further close the nutrient cycle.

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